Review of Palaeobotany and Palynology, 31 (1980/1981): 261—287
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands

ASPECTS OF LATE DEVONIAN AND EARLY CARBONIFEROUS PALYNOLOGY OF SOUTHERN IRELAND, IV MORPHOLOGICAL VARIATION WITHIN *DIDUCITES*, A NEW FORM-GENUS TO ACCOMODATE CAMERATE SPORES WITH TWO-LAYERED OUTER WALL

P.M. VAN VEEN

Laboratory of Palaeobotany and Palynology, State University, Utrecht (The Netherlands)

(Received February 25, 1980; revised version accepted May 1, 1980)

ABSTRACT

Van Veen, P.M., 1981. Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. IV. Morphological variation within *Diducites*, a new formgenus to accomodate camerate spores with two-layered outer wall. Rev. Palaeobot. Palynol., 31: 261—287.

In the Upper Devonian (Tournaisian 1a and 1b) of southern Ireland, camerate spores provided with a two-layered outer wall are regular components of palynological assemblages. These forms are attributed to the formgenus *Diducites* Van Veen nov. gen. The four species recognised [*D. plicabilis* Van Veen nov. spec., *D. versabilis* (Kedo) Van Veen, nov. comb. et emend., *D. poljessicus* (Kedo) Van Veen, nov. comb. et emend., and *D. mucronatus* (Kedo) Van Veen, nov. comb. et emend.] are linked in the *Diducites mucronatus* morphon, since they show continuous variation in morphology.

In the present paper the taxonomy of the individual species of this morphon and the application of the morphon in both biostratigraphy and phytogeography will be discussed.

INTRODUCTION

Upper Devonian and Lower Carboniferous rocks outcrop extensively in southern Ireland. In the southern part the sequence, of which the lithostratigraphy has been revised by Gardiner and Horne (1972, 1976), ranges in age from latest Givetian or earliest Frasnian (Clayton and Graham, 1974) into probable Namurian (Naylor et al., 1978).

Since 1971, the Laboratory of Palaeobotany and Palynology of the State University of Utrecht and the Geological Survey of Ireland have been cooperating in a project aimed at a better understanding of the geological history of southern Ireland during the Late Devonian and Early Carboniferous.

During the last few years, the author has been studying palynofloras in the more westerly sections of the counties Cork and Kerry. One of the sections, located at the southern shore of the Kenmare River, stretches from Ballycrovane Harbour to Kilcathrine Point and shows sediments of Late Devonian and Early Carboniferous age (Tn1—Tn2) in a near-continuous

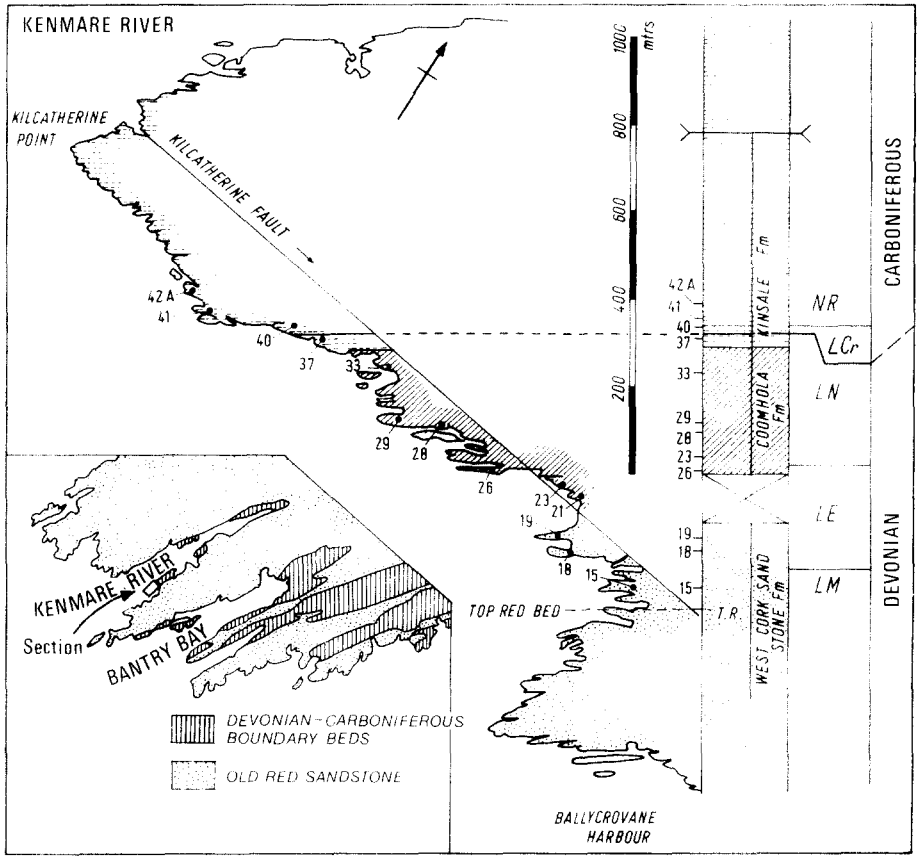


Fig.1. Map of Ballycrovane Harbour section, showing lithostratigraphy, position of samples and phases (Van der Zwan and Van Veen, 1978).

sequence (Fig.1). In the lower part of the section, in assemblages assignable to the LM to LCr phases of the *Retispora lepidophyta* assemblage zone (Van der Zwan and Van Veen 1978), one is confronted with a large number of spores characterised by the presence of a two-layered outer wall.

Species comparable in form and structure have only been sparsely described from earlier Devonian assemblages. In *Rhabdosporites parvulus* Richardson 1965, as well in ?*Calyptosporites* sp.A of Mortimer and Chaloner (1972), it is known that some specimens have three walls instead of two. The apiculate nature of their outer wall, however, does separate them from spores present in the Irish material. Much more comparable are species described and/or figured from the Upper Devonian elsewhere, such as *Hymenozonotriletes commutatus* Naumova 1953 figured by Andreeva in Prokovskaja (1966, part III, pl.39, fig.2), showing a specimen with an equatorial separation of the outer wall, *H. versabilis* Kedo 1957 as figured by Kedo et al. (1971, pl.XIV, figs. 6 and 7) and *H. mucronatus* Kedo 1974.

Streel (1969, p.5) mentioned a separation of the outer wall into two

layers in camerate spores in the Upper Devonian, when he remarks: ". . Parfois même une couche externe très finement plissée se détache de l'exoexine comme cela a été décrit par Allen pour le genre *Perotrilites* (*H. commutatus* Naum., *H. versabilis* Kedo)". This author (in Becker et al., 1974) also mentioned the presence of a "thin folded external part of the perine" in forms which he assigned to *Auroraspora* sp. cf. *Perotrilites perinatus* Hughes and Playford 1961.

It is here considered, however, that the two-layered nature of the outer wall is not in accordance with the generic diagnoses of *Hymenozonotriletes* Naumova ex Ishchenko 1952, *Auroraspora* Hoffmeister, Staplin et Malloy 1955 or of *Perotrilites* (Erdtman) Evans 1970.

A genus accomodating the description of the specimens present in the Irish material is not encountered in the *Genera File of Fossil Spores* (Jansonius and Hills, 1976 and supplements). Therefore, in the present paper the Irish forms will be formally described within the new formgenus *Diducites*, together with a discussion on their morphological variation and their presumed importance in latest Devonian stratigraphy and palaeogeography.

SYSTEMATICS

Formgenus *Diducites* Van Veen nov. gen.
Type species: *Diducites plicabilis* Van Veen, nov. spec.
Derivatio nominis: *diducere* (lat.): to part, to divide

Diagnosis

Spores trilete, camerate. Outer wall separated into two layers. Overall outline subcircular, roundly triangular, ovate to irregular.

Inner wall: Outline subcircular, roundly triangular, ovate to irregular, conformable or inconformable to overall outline; smooth, rigid or folded, no apparent intrastructure; wall thickness often indiscernable, rarely distinct; sutures of trilete mark almost extending to its equatorial outline, simple, or accompanied by slight thickenings or folds, usually distinct.

Inner layer of outer wall: Proximally attached to inner wall; outline subcircular, roundly triangular to ovate, conformable or inconformable to overall outline; homogeneous to intrastructured; internal margin badly to distinctly discernable, external margin clearly defined.

Outer layer of outer wall: Attached to, or partly to entirely detached from, inner layer; homogeneous to intrastructured, surface usually smooth; thickness often indiscernable, presumably very thin, probably slightly thicker above tetrad mark; recognisable by its relative translucency; folding and wrinkling frequently results in a more or less rugulate condition of the spores, proximal rugulae randomly to radially arranged, distal rugulae randomly to rarely radially arranged.

Comparison

Diducites nov. gen. can be recognised on the basis of a separation of the laevigate outer wall into two layers, showing a difference in translucency equatorially. In this respect the formgenus differs from superficially similar camerate genera, such as *Endosporites* (Wilson et Coe) Schopf, Wilson et Bentall, 1944 [characterized by a single, internally microreticulate outer wall (L.R. Wilson, pers. comm., 1977) or an internally smooth to irregularly reticulate, externally finely spinose outer wall (Brack and Taylor, 1972, p. 103)], *Spencerisporites* Chaloner 1951 (single-layered zona; see Leisman, 1962) and *Auroraspora* Hoffmeister, Staplin et Malloy 1955 (single, intra-structured finely granulose bladder; see Van der Zwan, 1980a). *Dibrochospor ites* Urban 1968 is reported to show an outer and an inner exoexine formed by two reticulae, differing from each other in mesh size.

Remarks

Heavy maceration, especially the use of strong oxidants, tends to remove the outer layer of the outer wall. Specimens thus produced show an outer wall morphology comparable to that of *Auroraspora*.

Diducites plicabilis Van Veen, nov. spec.

Holotype: Plate I, 7, 8, from BA-19, Ballycrovane Harbour. Slide BA-19/8, 108.0 × 33.3 on Leitz Ortholux 630124 (ACP).
Figured specimens: Plate I, 1—6; Plate II, 1—4; Plate III, 7, 10.

Diagnosis

Spores trilete, camerate. Outer wall separated into two layers. Overall outline commonly irregular, due to folding of the outer wall, to subcircular.

Inner wall: Generally inconformable to overall outline; smooth, commonly folded, folds generally do not show any preferred orientation, no apparent intrastructure; thickness indiscernable, probably very thin; sutures of trilete mark almost extending to its equatorial outline, simple, distinct to indistinct.

PLATE I (approximately × 800, unless otherwise indicated)

Diducites plicabilis sp. nov.

1, 3, 4. Equatorial compression, diameter 60 μm. 3a. Inner margin of inner layer of outer wall (× 1100). 3b. Outer margin of inner layer of outer wall (× 1100). 4. Continuity of outer layer of outer wall towards equator (× 1100).

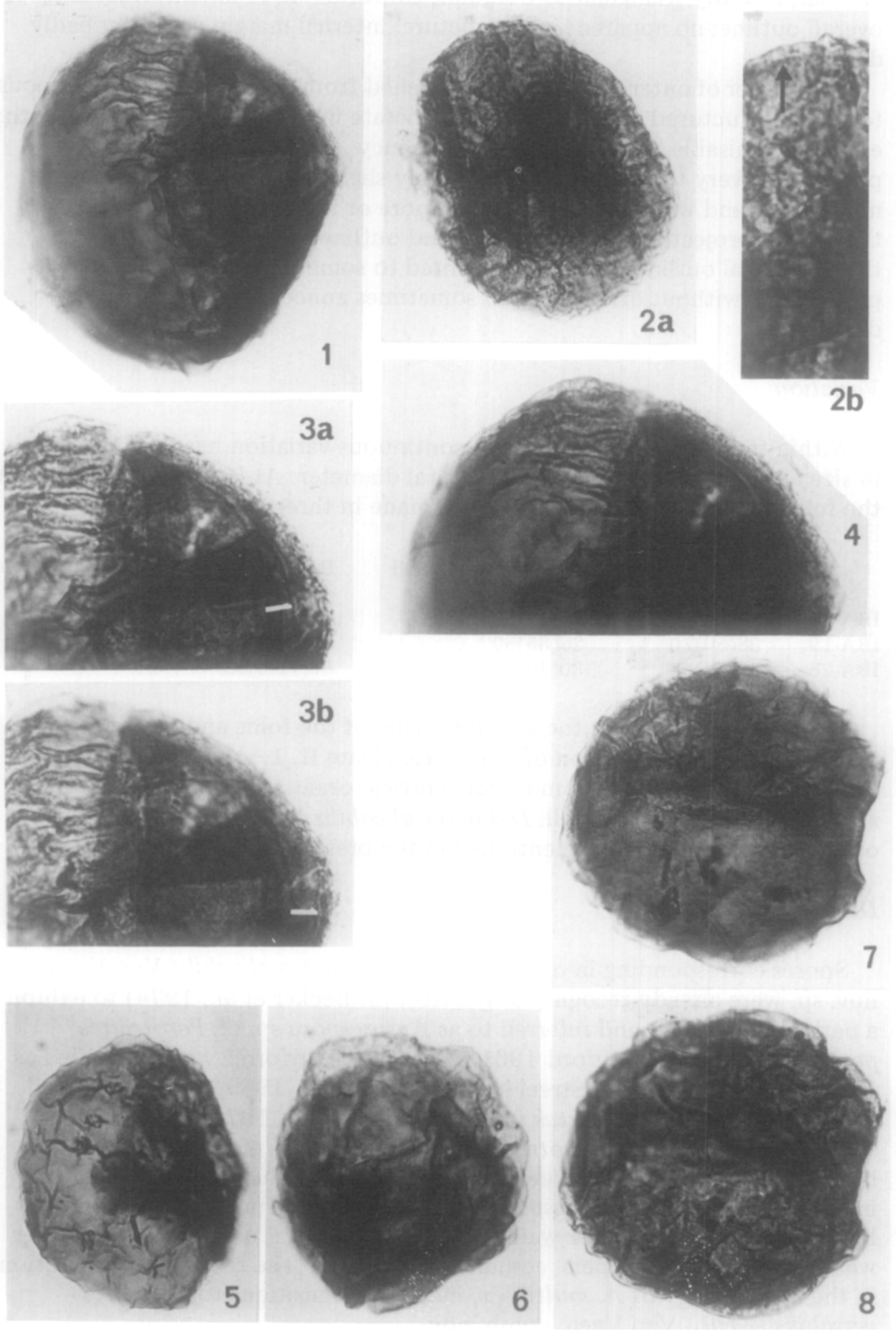
2. Specimen, diameter 53 μm, showing slight separation of outer wall layers (2b, approx. × 1400).

5. Specimen, 48 μm, showing crumpled inner wall.

6. Specimen, 48 μm, showing wide separation of outer wall layers.

7, 8. Holotype, 60 μm, proximal and 8, distal view.

PLATE I



Inner layer of outer wall: Proximally attached to inner wall; outline subcircular, roundly triangular to irregular, conformable to inconformable to overall outline; no apparent intrastructure; internal margin generally badly discernable.

Outer layer of outer wall: Usually detached from inner layer; homogeneous to (intra) structured — intrastructure punctate in polar view, surface smooth; easily recognisable by its relative translucency, thickness indiscernable, presumably very thin, sometimes probably slightly thickened above tetrad mark; folds and wrinkles resulting in a more or less rugulate condition of the spores, projecting up to 5 μm beyond outline inner layer and affecting the equatorial outline, randomly oriented to sometimes radially arranged proximally, without orientation to sometimes concentrically arranged distally.

Variation

Within the Irish material studied, continuous variation has been observed in size and ratio diameter inner wall/total diameter. At Ballycrovane Harbour the following measurements have been made in three samples:

	Total diameter	Diameter inner wall	Ratio	Number of spores
IBA-15	42(53.5)80 μm	27(40)60μm	51(75)94%	8
IBA-19	38(50)70	25(35)50	50(70)90	35
IBA-26	46(55)65	30(40)50	59(72.5)85	6

Variation also exists in the size and shape of the folds and wrinkles which cause the rugulate condition of the spores (Plate II, 1—4). Folds in the inner wall generally show a random to concentrical orientation and may severely affect the outline of this wall. *Diducites plicabilis* shows transitions to all other species of *Diducites* mentioned in the present paper (see p. 279).

Discussion

Spores corresponding in organisation to *Diducites plicabilis* Van Veen nov. sp. were already recognised by Streel (in Becker et al., 1974) to exhibit a perinal outer layer and referred to as *Auroraspora* sp. cf. *Perotrilites perinatus* Hughes et Playford 1961. Earlier, similar forms were identified as *Perotrilites* cf. *perinatus* (Streel in Bouckaert et al., 1969, pl.94, fig.2) and *Perotrilites* sp. cf. *P. perinatus* (Allen in Gayer et al., 1973, pl.15, fig.K). The original material of *Perotrilites perinatus* Hughes et Playford 1961, however, is clearly single-layered. Turnau (1975) included Streel's material in a new species, viz. *Auroraspora multiplex*. She did not recognise a two-layered nature of the outer wall and her holotype has a single-layered outer wall (E. Turnau, 1977, pers. comm.). Nonetheless, she recognised a variation in the morphology of *A. multiplex*, including transitions to *Diducites versabilis* (Kedo) Van Veen, comb. nov.

Winslow (1962) recorded *Calamospora obtecta* Winslow 1962, in contrast to the generic concept of *Calamospora*, to represent a perinate species; in one case an inner wall could be detected (Winslow, 1962, pl.17, fig.4). A re-evaluation of her material is necessary to decide whether her species is identical to *D. plicabilis*.

Comparison

The folded nature of both the inner wall and the outer layer of the outer wall constitutes the main differential character of *Diducites plicabilis* nov. sp. *D. mucronatus* (Kedo) Van Veen nov. comb. and *D. versabilis* have a rigid inner wall. *D. poljessicus* (Kedo) Van Veen has an unfolded to slightly folded outer layer of the outer wall. These folds do not project at the equator and do not affect the equatorial outline.

To elucidate the structure of *Diducites*, a single specimen of *D. plicabilis* preserved in equatorial compression will be described in detail. A drawing of this specimen, figured in Plate I, is presented in Fig.2.

The specimen has a nearly hemispherical distal side, whereas its proximal half is slightly angular towards the apex. The outer wall shows a thicker proximal and a thinner distal part.

At the proximal pole the inner wall can be seen to be very close to the outer wall (Plate I, 3a). It can be seen here that the inner layer of the outer wall has a distinct inner margin and shows a faint intrapunctation. Its thick-

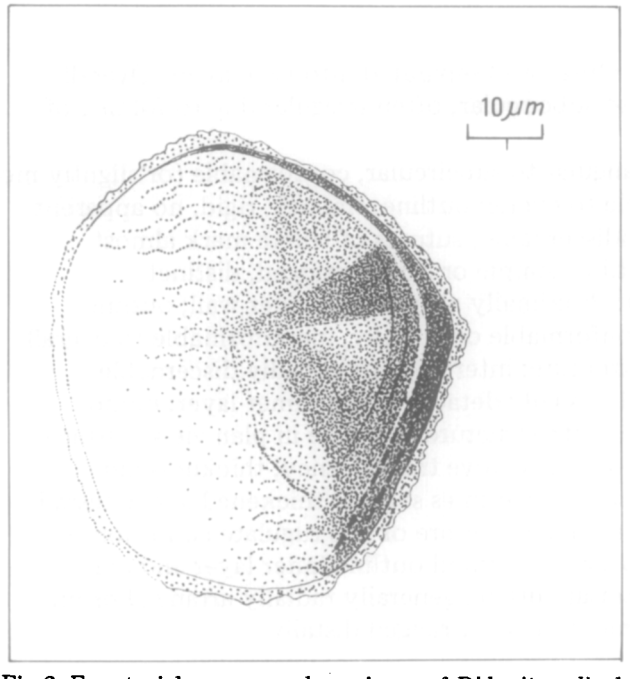


Fig.2. Equatorial compressed specimen of *Diducites plicabilis*, discussed in text (see also Plate I, 1, 3 and 4).

ness is 2.5 μm, decreasing towards the equator, where it measures less than 1 μm and looses its distinct inner margin.

There exists a distinct boundary between the inner and outer layer, caused by a sudden increase in intrastructure (punctate/granulate) within the outer layer, especially near the proximal pole (Plate I, 3b); near the equator the outer layer is far more translucent (Plate I, 4). The outer layer has a thickness of 2—3 μm at the pole, also decreasing towards the equator, where the outer layer is clearly separated from the inner layer, as is shown by the development of radially arranged folds (Plate I,4). At the distal hemisphere the inner and outer layer extend closely attached, as only minor folds are observed.

Size: 63 μm (equatorial) × 59 μm (polar).

Diducites versabilis (Kedo) Van Veen, comb. nov. et emend.

Basionym: *Hymenozonotriletes versabilis* Kedo 1957, Kedo, G.I.-Rep. Paleontol. Stratigr. Byelorussian S.S.R. 2: 25, pl.III, fig.4.
1971: *Hymenozontriletes tenuiextremis* Kedo in Kedo et al.
1974: *Rugospora versabilis* (Kedo) Streel in Becker et al.
1975: *Auroraspora versabilis* (Kedo) Turnau.

Holotype: Hymenozonotriletes versabilis Kedo 1957, pl.III, fig.4
Figured specimens: Plate II, 5, 6; Plate III. 1—6, 9

Emended diagnosis

Spores trilete, camerate. Outer wall separated into two layers. Overall outline roundly triangular to subcircular, often irregular due to folding of outer wall.

Inner wall: Roundly triangular to subcircular, conformable (or slightly more triangular) or inconformable to overall outline; smooth, rigid, no apparent intrastructure; thickness indiscernable; sutures of trilete mark almost extending to equatorial outline, simple or slightly ridged, distinct.

Inner layer of outer wall: Proximally attached to inner wall; outline triangular to subcircular, conformable or, usually, inconformable to overall outline; no apparent intrastructure; internal margin badly discernable.

Outer layer of outer wall: Usually detached from inner layer; homogeneous to intrastructured — intrastructure punctate in plan view, surface smooth; easily recognisable by its relative translucency; thickness indiscernable, presumably very thin, sometimes slightly thickened above tetrad mark; folds and wrinkles resulting in a more or less rugulate condition of the spores, projecting up to 12 μm beyond outline inner layer and consequently affecting the equatorial outline, generally radially arranged proximally, randomly to sometimes radially arranged distally.

Variation

Within the Irish material studied continuous variation has been encountered in size and ratio diameter inner wall/total diameter. At Ballycrovane Harbour the following measurements have been made in five samples:

	Total diameter	Diameter inner wall	Ratio	Number
IBA-15	42(48)55 μm	28(31)39 μm	55(65)82%	7
IBA-18	37(45)60	25(28)30	50(65)77	3
IBA-19	32(42)58	20(26)29	53(63)78	21
IBA-26	42(50)54	25(33)40	52(66)80	10
IBA-23	35(49)60	20(30)37	58(61)63	4
Kedo (1957)	50—60			
Kedo et al. (1971)	60—95	40—52		80
Turnau (1975)	61(76)106	37(61)63		11

Variation also exists in size and shape of the folds and wrinkles which cause the rugulate condition of the spore (Plate III, 3,4 and 6). In the area corresponding to the proximal surface of the inner wall, folds are sometimes more finely developed than outside this area. *Diducites versabilis* shows transitions to all other species of *Diducites* mentioned in the present paper (see p. 279).

Discussion

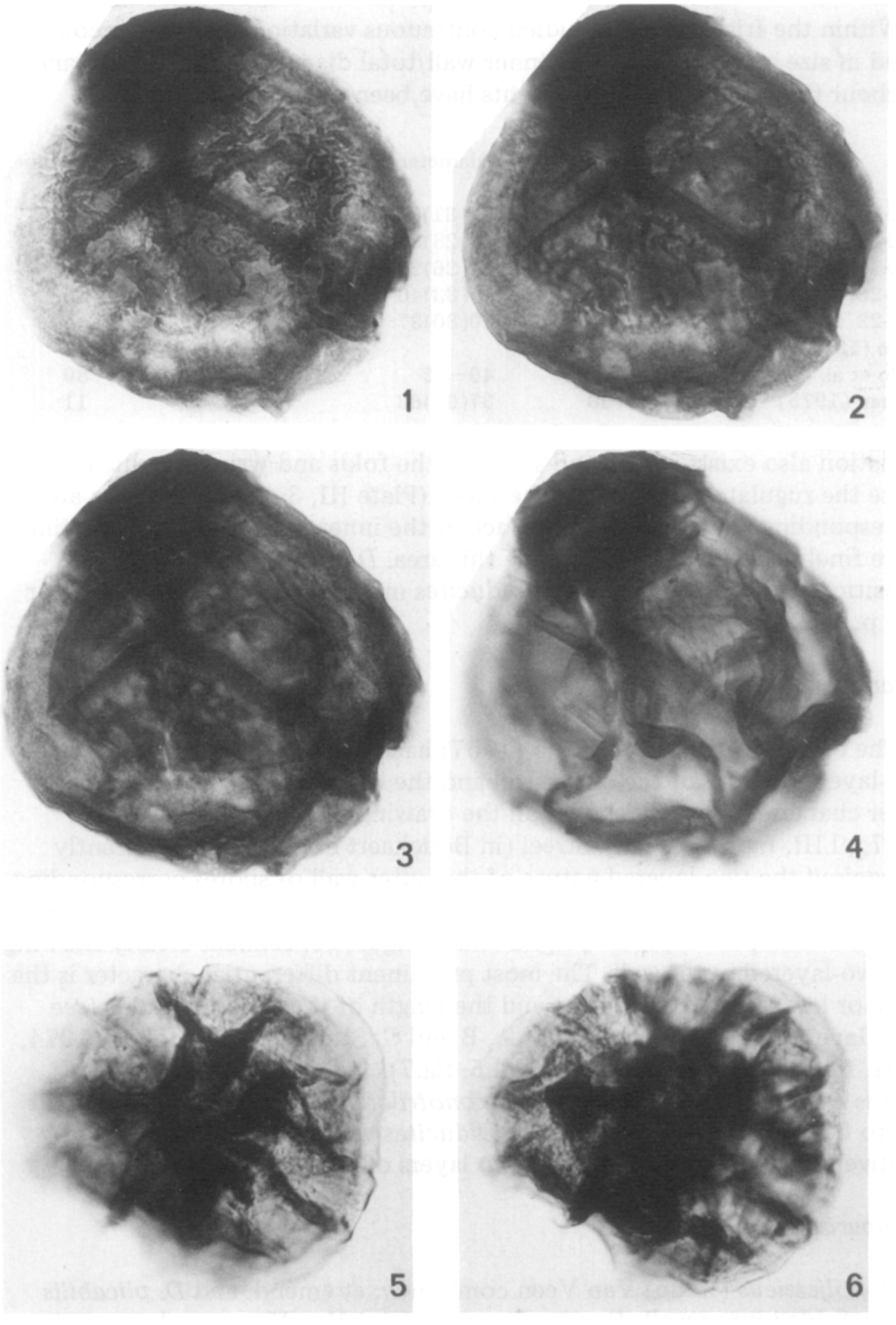
The original diagnosis of Kedo (1957) had to be emended because of the two-layered nature of the outer wall and the length of the suturae. The latter character is clearly shown on the drawing of the holotype (Kedo, 1957, pl.III, fig.4). Already Streel (in Bouckaert et al., 1968) apparently recognised the two-layered nature of the outer wall of spores corresponding to *Diducites versabilis* (Bouckaert et al., 1968, hors texte III, fig.6). Kedo (in Kedo et al., 1971 pl.XIV, figs.2 and 3) figured specimens clearly showing the two-layered outer wall. The most prominent differential character is the more or less radial arrangement and the length of the proximal folds (see also Gayer et al., 1973, pl.15, figs.A, B and C; Streel in Becker et al., 1974, pl.21, figs.2 and 5; Turnau, 1975, pl.5, fig.7).

It is here considered that *Hymenozonotriletes tenuiextremis* Kedo 1971 has to be regarded as a synonym of *Diducites versabilis*, in spite of its relatively wider separation of the two layers of the outer wall.

Comparison

D. poljessicus (Kedo) Van Veen comb. nov. et emend. and *D. plicabilis* have a folded inner wall; *D. mucronatus* (Kedo) Van Veen comb. nov. et emend. can be distinguished by its smooth or finely wrinkled outer layer, with wrinkles the length of which does not predominantly span the width of the camera.

PLATE II



Diducites poljessicus (Kedo) Van Veen comb. nov et emend.

Basionym: *Hymenzonotriletes poljessicus* Kedo 1957, Kedo, G.I. -Rep. Palaeontol. Stratigr. Byelorussian S.S.R., 2: 25, pl.III, figs.6, 7 and 8
1974: *Auroraspora poljessica* (Kedo) Streel in Becker et al.

Lectotype: Hymenozonotriletes poljessicus Kedo in IZV. Geol. Nauk, Akad. Nauk, B.S.S.R., No. 31/52: pl. III, fig. 6 (here designated)
Figured specimens: Plate IV, 1—4, 6

Emended diagnosis

Spores trilete, camerate. Outer wall separated into two layers. Overall outline roundly triangular to ovate or irregularly subcircular.

Inner wall: Outline subcircular, roundly triangular to irregular, usually inconformable to overall outline; smooth, commonly folded; wall thickness indiscernable, presumably thin; sutures of trilete mark almost extending to its equatorial outline, simple, often distinct.

Inner layer of outer wall: Proximally attached to inner wall; outline usually conformable to overall outline; no apparent (intra) structure; internal margin badly, external margin clearly defined; thickness indiscernable.

Outer layer of outer wall: Completely attached to inner layer of outer wall to partly detached; homogeneous or intrastructured — intrastructure punctate or reticulate in polar view; surface smooth; thickness indiscernable, presumably very thin; recognisable by its relative translucency; projecting up to 3 μm beyond outline inner layer; folds and wrinkles may result in a slight rugulate condition of the spores, not affecting the equatorial outline.

Variation

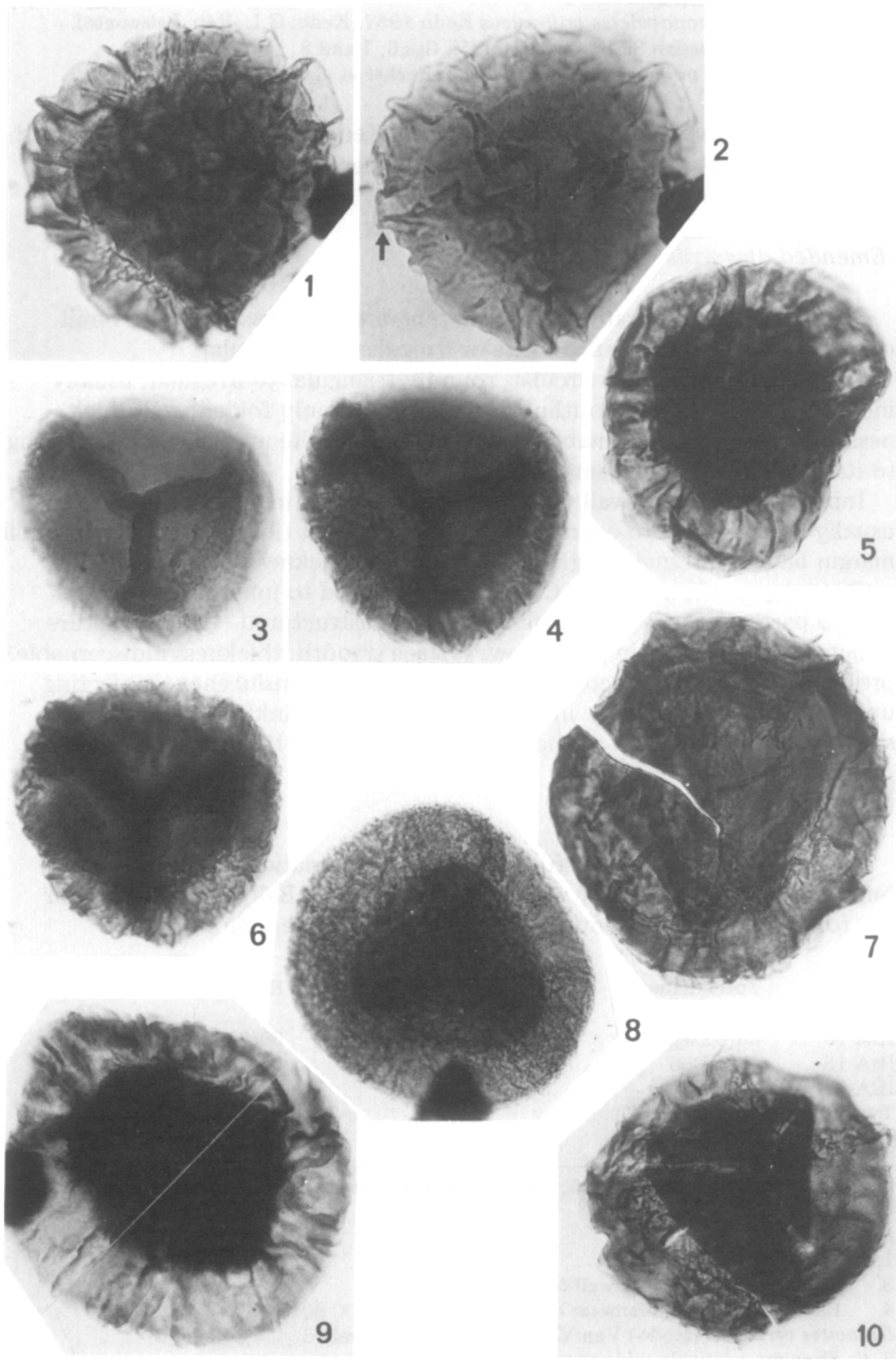
Within the Irish material studied continuous variation has been encountered in size and ratio inner wall/total diameter. At Ballycrovane Harbour the following measurements have been made in three samples:

	Total diameter	Diameter inner wall	Ratio	Number
IBA-15	38(62.5)80 μm	29(46)60 μm	56(73.5)84%	23
IBA-18	40(50)65	20(35)50	50(70)80	14
IBA-19	45(56)75	27(40)60	52(72)90	53
Type material (Kedo, 1957):	70—75 μm			

PLATE II (approximately × 800, unless otherwise stated)

Diducites plicabilis sp. nov.
1, 2. Proximal folds.
3. Equatorial view, inner wall folds.
4. Large distal folds, diameter of outer wall 60 μm (× 900).
Diducites versabilis (Kedo) Van Veen, comb. nov. et emend.
5, 6. Showing relatively wide separation of outer wall layers.

PLATE III



Folds in the inner wall have a concentrical to random orientation, their length often equals the diameter of the inner wall. *Diducites poljessicus* shows transitions to all other species of *Diducites* in the present paper (see p. 279).

Discussion

The diagnosis is emended because of the two-layered nature of the outer wall in the Irish material, the length of the suturae and the generally folded nature of the inner wall. The latter character is clearly shown in one of the drawings of *Hymenozonotriletes poljessicus* provided by Kedo (1957, pl.III, fig.6). Since Kedo did not clearly select a holotype, this drawing is here chosen to represent the lectotype. *Hymenozonotriletes* cf. *variabilis* Naumova 1953 in Caro-Moniez (1962, pl. XVII, fig. 6) as well as aff. *Velosporites* sp. in Streel (1964, pl.1, fig.13) show the characteristics of *D. poljessicus*. *Hymenozonotriletes compactus* Nekrjata 1971 and particularly *H. callosus* Kedo 1974 may show a close relationship to *D. poljessicus*. However, the presence of a two-layered outer wall has to be more conclusively established before counting these species as synonyms of *D. poljessicus*. In this respect it should be noted that Kedo et al. (1971, p. 39) already remarked that *H. callosus* should be regarded as belonging to a separate morphological group of spores.

Comparison

In specimens which do not show many folds, the structure of the outer wall of *D. poljessicus* resembles that of *D. mucronatus* (Kedo) Van Veen comb. nov. et emend.

This latter form as well as *D. versabilis* have a rigid inner wall and differ also by their generally smaller ratio inner wall/total diameter. *D. versabilis* and *D. plicabilis* have a folded outer layer of the outer wall, of which the folds often clearly project beyond the equatorial outline of the inner layer and affect the equatorial outline.

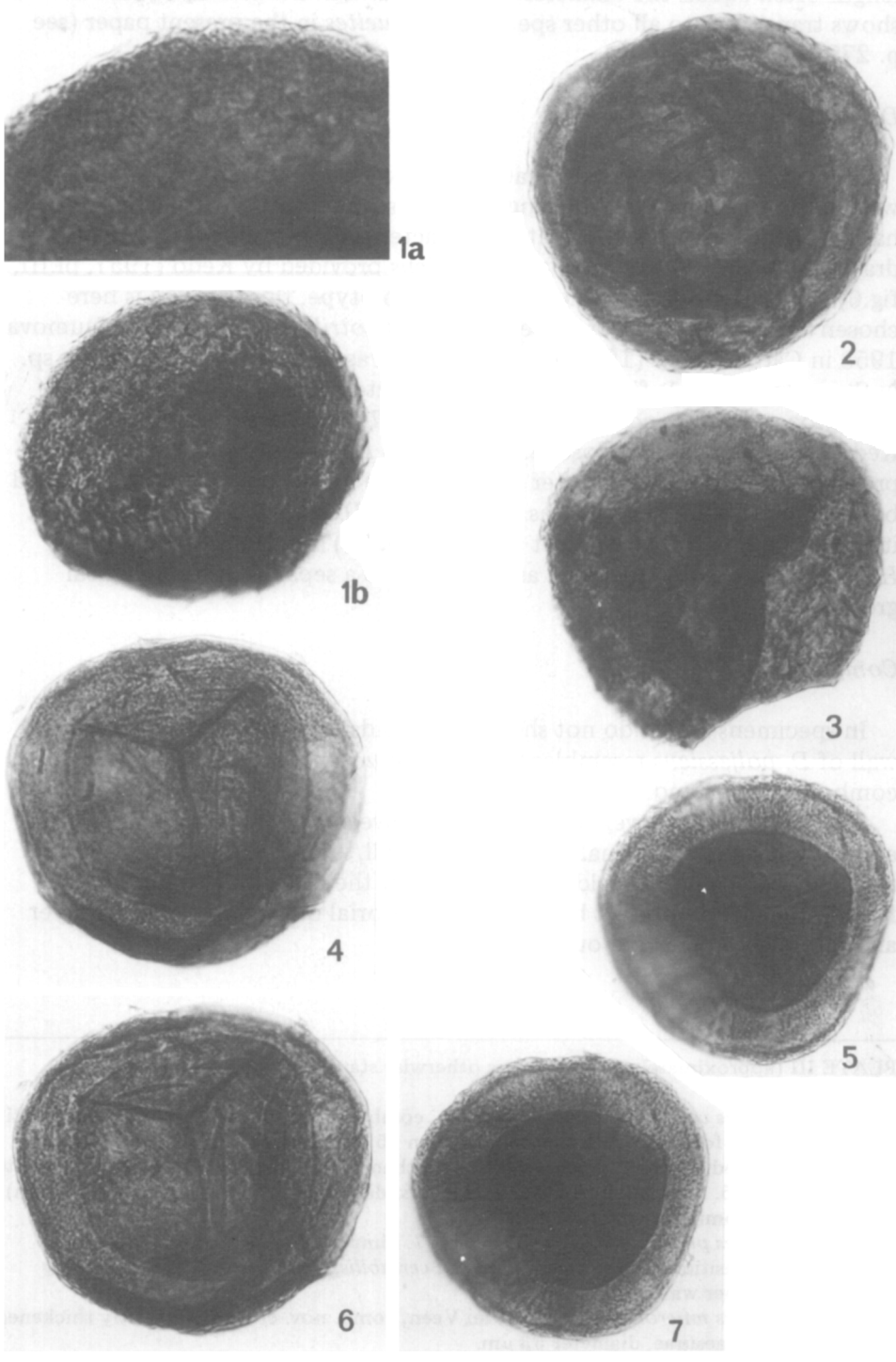
PLATE III (approximately × 800, unless otherwise stated)

1–6, 9. *Diducites versabilis* (Kedo) Van Veen, comb. nov. et emend. 1, 2. Showing continuity of folds around equator, specimen 55 μm. 3. Laesurae, slightly folded or thickened. 4. Slightly coarser proximal than 6, distal folds in outer layer, diameter 47 μm. 5. Separation of outer wall layers, diameter 55 μm. 9. Specimen (55 μm) with prominent radial folds (× 900).

7, 10. *Diducites plicabilis* Van Veen, sp.nov. 7. Simple laesurae, diameter 66 μm. 10. Transitional specimen towards *D. versabilis*, slightly folded and relatively wide inner wall, 54 μm.

8. *Diducites mucronatus* (Kedo) Van Veen, comb. nov. et emend. slightly thickened around laesurae, diameter 53 μm.

PLATE IV



Diducites mucronatus (Kedo) Van Veen, comb. nov. et emend.

Basionym: *Hymenozonotriletes mucronatus* Kedo, 1974, in: V.K. Golubtsov and S.S. Manjkin (Editors): Paleozoic Spores of Byelorussia (Pripyat Depression), NIGRI, Minsk, p.40, pl.X, figs.11—13
1953: *Hymenozonotriletes commutatus* Naumova non *H. commutatus* (Waltz) Ishchenko 1952
1974: *Hymenozonotriletes explicatus* Kedo
1977: *Auroraspora commutata* (Naumova) Keegan

Holotype: Hymenozonotriletes mucronatus Kedo 1974, pl.X, fig.11
Figured specimens: Plate III, 8; Plate IV, 5, 7; Plate V, 1—6

Emended diagnosis

Spores trilete, camerate. Outer wall two-layered. Overall outline subcircular to rounded triangular.

Inner wall: Outline subcircular to rounded triangular, conformable to overall outline or slightly more triangular; smooth, rigid; wall thickness up to 2 μm, commonly indiscernable; no apparent intrastructure; sutures of trilete mark almost extending to its equator, simple or accompanied by thickenings or folds, commonly distinct.

Inner layer of outer wall: Proximally attached to inner wall; outline usually conformable to overall outline; no apparent (intra) structure; internal margin badly, external margin clearly discernable.

Outer layer of outer wall: Completely attached to inner layer of outer wall or partly detached; homogeneous or intrastructured — intrastructure punctate or reticulate in plan view; surface smooth; thickness indiscernable, presumably very thin, recognisable by its relative translucency, projecting 0.5—4 μm beyond outline inner layer; folds and wrinkles may result in a more or less rugulate condition of the spore.

Variation

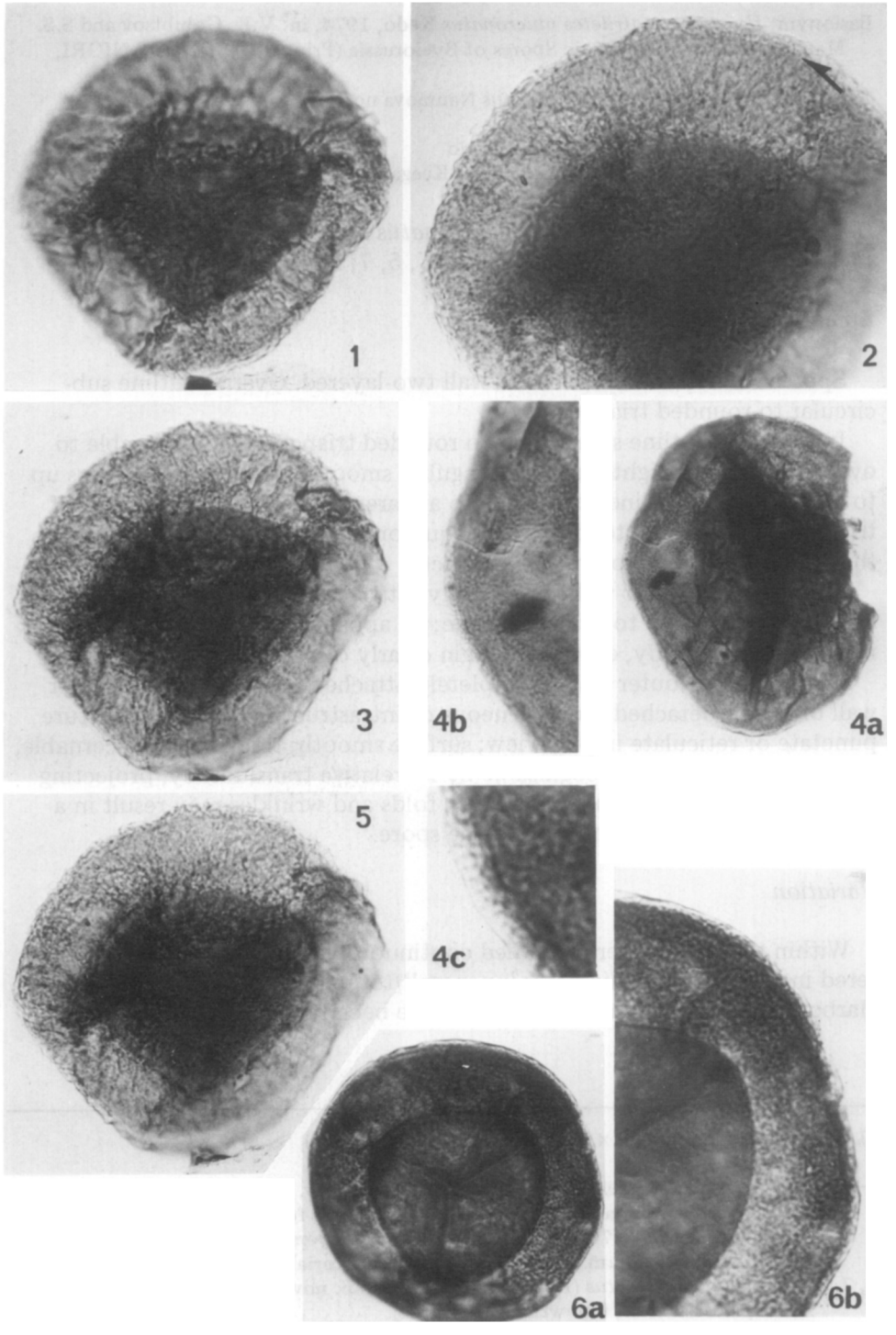
Within the Irish material studied continuous variation has been encountered in size and ratio diameter inner wall/total diameter. At Ballycrovane Harbour the following measurements have been made in four samples:

PLATE IV (approximately × 800, unless otherwise stated)

1—4, 6. *Diducites poljessicus* (Kedo) Van Veen, comb. nov. et emend. 1a. Detail, separation of outer wall layers, × 1400. 1b. Transitional form towards *D. plicabilis*, diameter 70 μm, × 700. 2. Showing outer wall layers, diameter 64 μm. 3. Proximal view, diameter 60 μm. 4. Proximal and 6, equatorial view, diameter 65 μm.

5, 7. *Diducites mucronatus* (Kedo) Van Veen, comb. nov. et emend. 5. Proximal view. 7. Equatorial view, fine wrinkles.

PLATE V



	Total diameter	Diameter inner wall	Ratio	Number
IBA-15	35(52)65 μm	23(31)40 μm	49(61)68%	7
IBA-18	45(51)60	25(30)35	50(59)67	11
IBA-19	36(48.5)70	23(30)37	48(62)75	61
IBA-26	45(55)65	25(31)39	49(57)63	9

In samples from other areas of southern Ireland, the total diameter may be considerably larger, e.g. in Hook Head, where specimens up to 90 μm can be regularly found. An important variation also exists in the size and shape of the folds and wrinkles, which often cause a rugulate condition of the outer layer of the outer wall. Proximally, folds and wrinkles are randomly distributed to radially arranged. More or less radially arranged, large folds (as in the type material of *Hymenozonotriletes commutatus* Naumova) may sometimes be present; these folds do not affect the equatorial outline. Distally, folds and wrinkles do not show any preferred orientation. Small crescent-shaped folds may be present at the ends of the rays in the inner wall (as cited by Kedo, 1974 for *Hymenozonotriletes mucronatus*), but do not affect the "rigid" outline.

Diducites mucronatus shows transitions to all other species of *Diducites* described in this paper (see p. 279).

Discussion

In the description of *Hymenozonotriletes commutatus*, Naumova (1953, p.113) mentioned a variable structure and sculpture of the outer wall: "membranous, warty or chagrinate with crumpled folds". A two-layered nature of the outer wall cannot be deduced from the original illustrations (Naumova, 1953, pl.17, figs.12 and 13, present paper Fig.3a). Subsequently, however, Kedo (1957, pl.II, fig.10) figured *H. commutatus* showing a (?translucent) small ring around the equator (present paper, Fig. 3b). A specimen figured by Andreeva (in Pokrovskaja, 1966, vol.III, pl.39, fig.2; present paper Fig.3c) clearly shows the same phenomenon. Although never specifically stated, these illustrations may indicate that the present Russian concept of the species is in accordance with a two-layered nature of the outer wall. Moreover, identifications of *H. commutatus* in the Russian literature show a relatively wide range of intraspecific variation, especially

---

PLATE V (approximately × 800, unless otherwise stated)

Diducites mucronatus (Kedo) Van Veen, comb. nov. et emend.

1—3, 5. Specimen 77 μm. 1. Proximal view, laesurae. 2. Detail, separation of outer wall layers (× 1000). 3. Proximal view, radially arranged wrinkles and small folds. 5. Equatorial—distal view.

4. a. Equatorial view, diameter 57 μm. b. Details, separation of outer wall layers, intrastructure (× 1400). c. Detail, width of outer layer 1.5 μm (× 2800).

6. a. Proximal—equatorial view, specimen 56 μm. b. Intrastructure and separation of outer wall layers (× 1400).

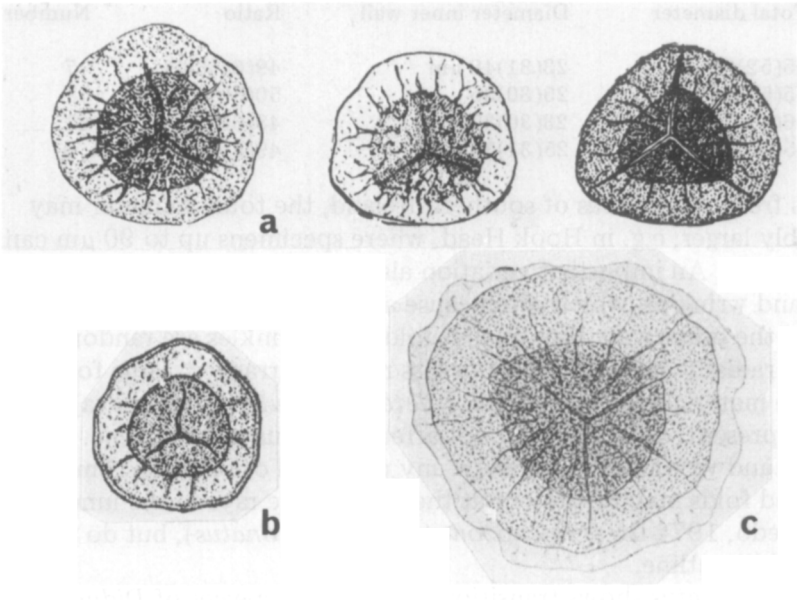


Fig.3. Figured specimens of *Hymenozonotriletes commutatus* Naumova 1953 in Russian literature: a, Naumova (1953); b, Kedo (1957); c, Andreeva (1966).

with regard to the size and nature of the folds. The rather prominent radially arranged folds as pictured by Naumova are not necessarily a primary identifying characteristic of the species (compare Nekrjata 1974, pl.XXII, 5 and 6; Avkhimovits 1974, pl.XXX, fig.5, pl.XXXII, fig.8, pl.XXXIII, fig.6). Thus, it is here believed that the present material can be well identified in terms of *H. commutatus* Naumova. The name *H. commutatus* Naumova, however, is illegitimate, since it is a later homonym of *H. commutatus* (Waltz) Ishchenko 1952.

Other available epithets can be found in the work of Kedo (1974), who established two new species to accomodate forms which can well be included in the range of variation of *H. commutatus* Naumova, viz. *H. mucronatus* and *H. explicatus*. Since the presence of a two-layered outer wall is more clearly detectable in the illustrations of *H. mucronatus* (Kedo, 1974, pl.10, figs.11—13), the present author favours the further application of this name rather than *H. explicatus*.

Comparison

Diducites poljessicus and *D. plicabilis* differ from *D. mucronatus* in possessing a generally folded inner wall as by their larger ratio diameter inner wall/total diameter. *D. versabilis* has a more or less dense and dominant ornamentation of radially arranged folds. These folds usually span the width of the camera and affect the equatorial outline.

THE *DIDUCITES MUCRONATUS* MORPHON

In order to clarify the morphological interrelationships between *Diducites plicabilis*, *D. versabilis*, *D. poljessicus* and *D. mucronatus*, these species are united in the *Diducites mucronatus* morphon. A morphon constitutes a non-typological classification unit, defined as a group of palynological species united by continuous variation of morphological characteristics (Van der Zwan, 1979).

Common characteristics of this *Diducites mucronatus* morphon are:

(1) Separation of the outer wall into two layers.

(2) Laesurae never exceed the inner wall radius.

Variable characteristics of this morphon are:

(1) Inner wall features: (a) rigid or folded; (b) outline rounded triangular to subcircular to irregular.

(2) Outer wall features: (a) continuous variation in degree of wrinkling or folding of outer layer of outer wall, to apparently smooth; (b) outline: outer layer rounded triangular to subcircular, ovate to irregular, inner

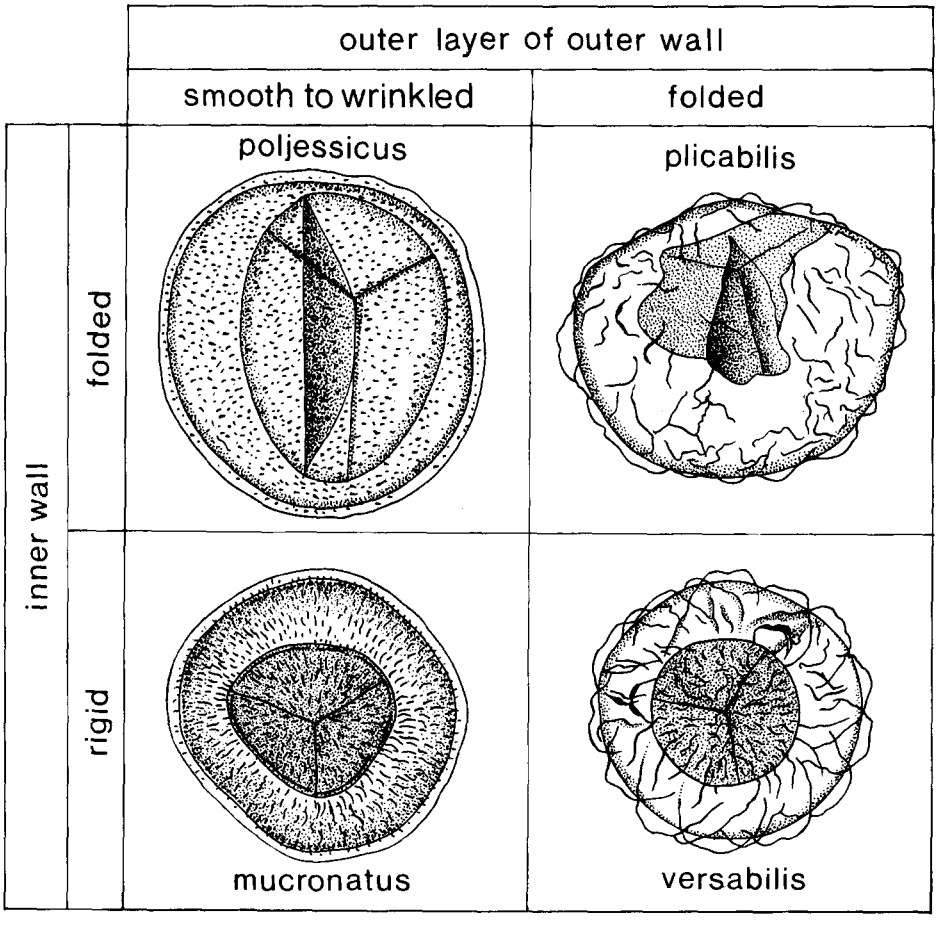


Fig.4. Classification scheme of *Diducites* spp.

layer triangular, subcircular to ovate; and (c) degree of separation of layers of outer wall.

(3) Ratio diameter inner wall/total diameter:

Diducites plicabilis	BA-19	50(70) 90%	35 specimens
Diducites versabilis	BA-19	53(63) 78%	21 specimens
Diducites poljessicus	BA-19	52(72) 90%	53 specimens
Diducites mucronatus	BA-19	48(62) 75%	61 specimens

It is here proposed to classify the specimens of *Diducites* on the basis of the variable characteristics 1a and 2a, with 3 as an important accessory variable (Fig.4 shows the classification).

Comparison of the Diducites mucronatus morphon

The *Diducites mucronatus* morphon associates apparently unrelated, but widely known species, which are often mentioned separately in the numerous references concerning Late Devonian palynology.

In search for species showing morphological relationships to the morphon, the author came across a taxon described by Kedo from the Upper Frasnian from the U.S.S.R. as *Hymenozonotriletes radiatus* Naumova 1953 var. *poljessicus* Kedo 1971 (in Nazarenko et al., 1971, p.166).

The morphological similarity is indicated by comparison of the following features:

(a) From an interpretation of the figured specimens (Nazarenko et al., 1971, Pls.VII, VIII and IX) it can be concluded that the variation in the morphology of the inner wall of this species resembles that of the morphon: the inner wall can be rigid (Nazarenko et al., 1971, pl.IX, figs.1—3) to folded (ibid, pls.VII and VIII, figs.1—8, except 7). The ratio inner wall/outer wall diameter is also comparable.

(b) According to the description of Kedo, the outer wall ("perispore") is ornamented with closely spaced, 3—4 μm long, up to 2 μm thick "brushes" ("chtchetinkami"). On the basis of the several figured specimens, however, it may be concluded that these "brushes" represent small folds, comparable in size and nature to those observed in specimens of the *D. mucronatus* morphon.

(c) From the description as well as from the figured specimens, the presence of separated outer wall-layers cannot be concluded with certainty (but see Nazarenko et al., 1971, pl.VII, fig.9 and pl.IX, fig.6 which show suggestive features).

In conclusion, the author is of the opinion that a critical re-evaluation of the Russian material may be rewarding, when it comes to tracing the *Diducites mucronatus* morphon back in the Devonian.

Another taxon, probably comparable to the *D. mucronatus* morphon is described from the Famennian of Western Australia as *Leiozonotriletes laurelensis* Balme et Hassell 1962. Morphological similarity is only indicated

by the presence of a "limbus" in the outer wall of these camerate spores, however. Again, a critical re-evaluation of this taxon is needed to trace the morphon in Australia.

STRATIGRAPHICAL DISTRIBUTION OF *DIDUCITES*

The concept of the *Diducites mucronatus* morphon has been based on material derived from samples of latest Devonian deposits of the Ballycrovane Harbour section and the Kerry Head (Ballyheigue) section in western Ireland (Bridge et al., 1980). Application of the scheme of compositional development of Late Devonian—Early Carboniferous palynological assemblages, reconstructed by Van der Zwan and Van Veen (1978) and Van der Zwan (1980b) shows that these deposits can be correlated with the LM (former LC), LE, LN and LCr phases of the *Retispora lepidophyta* assemblage zone (Fig.1). Only a few specimens of *Diducites versabilis* were recorded in assemblages of the NR phase of the *Verrucosisporites nitidus* assemblage zone. In Fig.6 relative abundancies of the various constituents of the *Diducites mucronatus* morphon as well as of *Retispora lepidophyta* are placed alongside a generalised lithological column as recognised in the Ballycrovane Harbour section.

Comparison with other data from Ireland

Higgs (1975) recorded *D. versabilis*, *D. mucronatus* (as *Hymenozonotriletes commutatus*) and *D. poljessicus* in PL assemblages from Hook Head. The latter form was also recorded in the lowest VI sample of this section. Work of Higgs in Naylor et al. (1977) on the south Dunmanus Bay section, Keegan (1977) in the Galley Head—Leap Harbour area, southwest Ireland and Van der Zwan (1980b) in the Bantry Bay area, does not change the picture from Ballycrovane Harbour, that *Diducites* spp. disappear approximately together with *Retispora lepidophyta.* Spores belonging to the *Diducites mucronatus* morphon were not mentioned by Clayton et al. (1974), but are now known to be present in LL, LE and LN assemblages from the sections studied in the latter paper (K. Higgs, pers. comm.).

Occurrences of Diducites outside Ireland

From outside Ireland only the most important and complete successions where *Diducites* spp. are present will be discussed in some detail:

(a) In the Ardennes area the succession of palynological assemblages has been firmly established by Streel (e.g., in Bouckaert et al., 1968; in Becker et al., 1974 and in Clayton et al., 1977). The *Diducites mucronatus* morphon, present as *D. versabilis*, *D. plicabilis* (identified as, e.g., *Auroraspora* sp. cf. *Perotrilites perinatus* Hughes et Playford 1961), and *D. poljessicus*, occurs in the Famennian (Fa1, Fa2) and the lower part of the Tournaisian (Tn1); quantitatively the morphon is an important constituent of Fa2c assemblages.

In contrast to the situation in southern Ireland, a joint disappearance of *Diducites* and *Retispora lepidophyta* cannot be demonstrated in the Ardennes.

(b) From the Pripyat Depression in the U.S.S.R., Kedo et al. (1971) described assemblages dominated by spores assignable to the *Diducites mucronatus* morphon, particularly from the Lebedyan beds (spore zone I). *Retispora lepidophyta* enters at the base of the Dankov beds (spore zone II) and dominates the higher assemblages (spore zone III). Subsequent work of Avkhimovits (1974) substantiated this picture.

(c) In a recent paper, Streel and Traverse (1978) described spore assemblages from a Devonian—Mississippian transition sequence near Altoona, Penn., U.S.A. The morphon is represented here by *D. poljessicus* (identified as *Auroraspora poljessica*; samples 1, 2 and 3), *D. plicabilis* (samples 1, 2 and 4), *D. versabilis* (samples 1, 2 and 3) and probably *D. mucronatus* (identified as *Endosporites chagrinensis*, and compared with *D. versabilis* by Streel and Traverse; samples 1, 2 and 3).

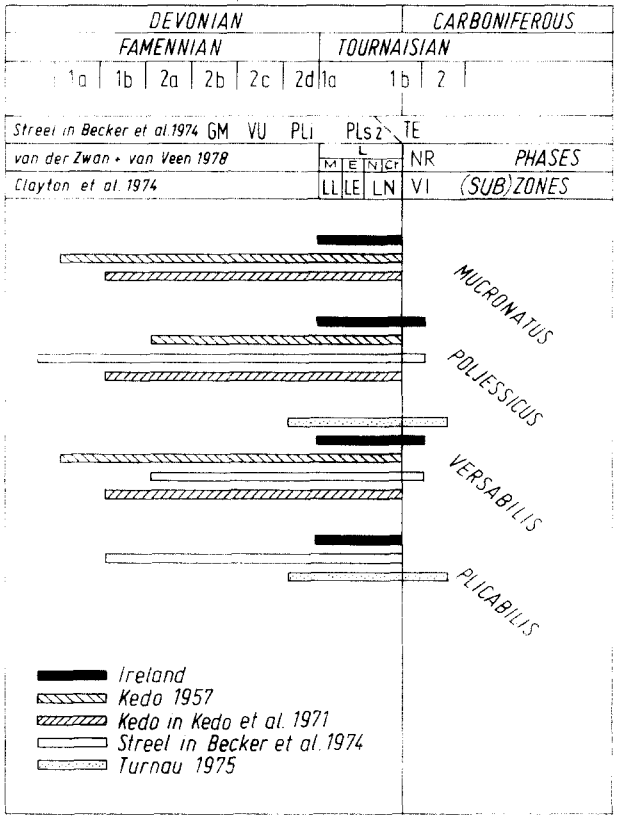


Fig.5. Stratigraphical distribution of *Diducites* spp.

Discussion

The stratigraphical extent of the species assigned to *Diducites* is summarised in Fig.5. From this picture it may be concluded that the identification of *Diducites* spp. in palynological assemblages generally indicates a Late Devonian (Famennian to Tournaisian (Tn1)) age.

If a closer morphological relationship between the *Diducites mucronatus* and *H. radiatus* Naumova 1953 var. *poljessicus* Kedo 1971 can be substantiated, the range of the morphon would be extended downwards to within the Late Frasnian.

From the comparison of the most complete sequences we might conclude that the palynological succession in the latest Devonian of the Northern Hemisphere may be characterised by: (1) a dominance of the *Diducites mucronatus* morphon in the Fa2b and 2c; (2) the subsequent appearance and dominance of *Retispora lepidophyta* in the Fa2d and Tn1a; and (3) the rapid disappearance of *Retispora lepidophyta*, frequently in combination with the disappearance of the *Diducites mucronatus* morphon.

At first sight, the palynological succession in the Ballycrovane Harbour section seems to fit well with this generalised picture (Fig.6). However, the change in dominance of *Diducites* spp. towards *Retispora lepidophyta* cannot be reconciled chronostratigraphically with the situation elsewhere. The change in dominance occurs in the transition between the LE and LN phases (Fig.1). On the basis of the presence of *Hymenozonotriletes explanatus*, the LE phase has to be correlated with the uppermost Tn1a and lowest Tn1b (compare Streel in Paproth and Streel, 1970; Clayton et al., 1977). Thus, the change in dominance in the Ballycrovane Harbour section occurs later than, e.g., in the Ardenno-Rhenish Basin.

PALAEOGEOGRAPHICAL SIGNIFICANCE

It is here considered that the shift in dominance of *Diducites* spp. towards *Retispora lepidophyta* in the Ballycrovane Harbour section could well be the

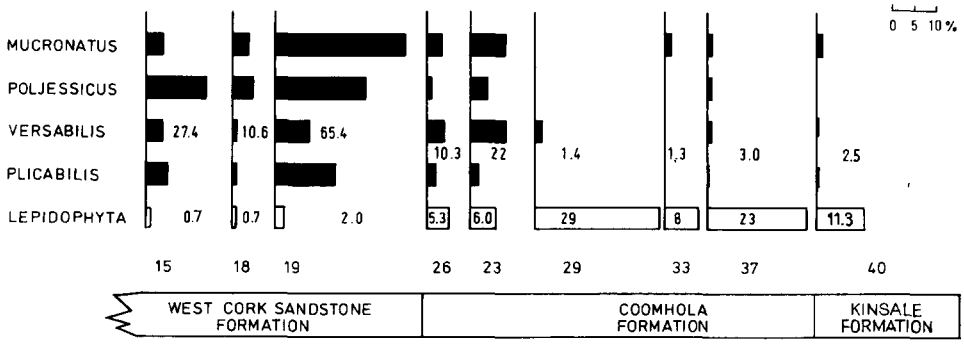


Fig.6. Quantitative distribution of *Diducites* spp. (total percentage indicated) versus *Retispora lepidophyta* in relation to lithostratigraphy.

result of a palaeogeographical change. The change in dominance clearly coincides with a change in lithology: samples 15—19 were derived from the West Cork Sandstone Formation, of which the sediments were deposited by rivers on the alluvial plain, whereas samples 26—40 are derived from the Coomhola and lowest part of the Kinsale Formation, which are thought to represent coastal to marine deposits (see Fig.6). The *Diducites* and *Retispora lepidophyta* dominant assemblages could therefore well be interpreted in terms of environmentally influenced associations: *Diducites* related to an environment related to the alluvial plain, *Retispora lepidophyta* related to an environment related to the coastal area during the LE and LN phases (Van der Zwan and Van Veen, 1978).

Within this context it is interesting to note that according to Kedo (in Nazarenko et al., 1971, p.167), *H. radiatus* Naumova 1953 var. *poljessicus* Kedo 1971 "evidently is characteristic for terrigeneous deposits, where they are present in large numbers".

The regional and interregional implications of such environmentally controlled dominances can only be estimated when comparable data from other sections are available. At present the implications for the whole of southern Ireland are being investigated by the author in collaboration with C.J. van der Zwan.

BOTANICAL AFFINITIES

Spores of *Diducites* nov. gen. have not been described *in situ* in references concerning Late Devonian palaeobotany. Therefore, the botanical affinities of the taxon remain uncertain. From the abundance of these forms in Late Devonian alluvial deposits, it can be concluded that the parent plant of *Diducites* has been an important constituent of the Late Devonian flora or delivered its spores in great numbers, probably to overcome the special circumstances in the alluvial plain area in an arid climate.

CONCLUSIONS

(1) The occurrence in the Upper Devonian of a group of spores, *Diducites* nov. gen., showing a smooth, two-layered outer wall, seems well established.

(2) The four species recognised [*D. plicabilis* Van Veen nov. sp., *Diducites versabilis* (Kedo) Van Veen, nov. comb. et emend., *D. poljessicus* (Kedo) Van Veen, nov. comb. et emend., and *D. mucronatus* (Kedo) Van Veen, nov. comb. et emend.] are linked by continuous variation in terms of a morphon (*Diducites mucronatus* morphon). The variation within the *D. mucronatus* morphon could well represent a natural variability pattern of spores of a single plant taxon, thus the total of the elements of the morphon in individual assemblages may represent palynodemes (Visscher, 1971).

(3) The presence of *Diducites* spp. is an indication of a latest Devonian (Famennian—earliest Tournaisian 1b) age, but if identification of *Hymenozo-*

notriletes radiatus Naumova 1953 var. *poljessicus* Kedo 1971 with the *D. mucronatus* morphon can be verified, the range can be extended into the Late Frasnian.

(4) Throughout Europe one may recognise a change in dominance between the *D. mucronatus* morphon and *Retispora lepidophyta* in the Latest Devonian. This change, however, is by no means contemporaneous.

(5) Apart from the influences of the interregional, time-proportionate compositional development of palynological assemblages, the change in dominance may also be largely influenced by local differences in palaeogeography.

(6) The botanical affinity of *Diducites* is as yet unknown.

ACKNOWLEDGEMENTS

The author wishes to thank Dr. H. Visscher and Prof. F.P. Jonker for their guidance. He is very grateful to Dr. C.J. van der Zwan for many stimulating discussions, as well as to Prof. J.B. Richardson (British Museum, London) and Prof. M. Streel (Université de Liège) for their comments on the subject during various stages of the research. Furthermore, acknowledgements are extended to Mr. T. Schipper, Mr. W. Scheepmaker and Mr. H. Rijpkema for drawing the diagrams and to Mr. H.A. Elsendoorn for preparing the microphotographs.

Thanks are due to the Niels Stensen Stichting (Amsterdam) for important financial support during the academic year 1978/1979.

REFERENCES

Andreeva, E.M., 1966. Devonian spore and pollen complexes of the U.S.S.R. In: I.M. Pokrovskaja (Editor), Palaeopalynology. Min. Geol. S.S.R., Tr. VSEGEI, N.S., 141(1): 33—53; 141(3): 64—84 (in Russian).

Avkhimovits, V.I., 1974. Palynological characteristics of the Upper Famennian saline beds of the Pripyat Basin. In: V.K. Golubtsov and S.S. Manjkin, (Editors), Paleozoic Spores of Byelorussia (Pripyat Depression). NIGRI, Minsk, pp. 95—107 (in Russian).

Balme, B.E. and Hassell, C.W., 1962. Upper Devonian spores from the Canning Basin, Western Australia. Micropaleontology, 8: 1—28.

Becker, G., Bless, M.J.M., Streel, M. and Thorez, J., 1974. Palynology and ostracod distribution in the Upper Devonian and basal Dinantian of Belgium and their dependence on sedimentary facies. Meded. Rijks Geol. Dienst, N.S., 25: 9—99.

Bouckaert, J., Streel, M. and Thorez, J., 1968. Schéma biostratigraphique et coupes de référence du Famennien belge. Ann. Soc. Géol. Belg., 91: 317—336.

Bouckaert, J., Streel, M., Thorez, J. and Mound, M.C., 1969. Biostratigraphic chart of the Famennian stage (Upper Devonian) in the type localities of Belgium: a preliminary report. J. Paleontol., 43(3): 727—734.

Brack, S.D. and Taylor, T.N., 1972. The ultrastructure and organisation of *Endosporites*. Micropaleontology, 18: 101—109.

Bridge, J.S., Van Veen, P.M. and Matten, L.C., 1980. Aspects of the sedimentology, palynology and palaeobotany of the Upper Devonian of southern Kerry Head, Co. Kerry, Eire. J. Geol., in press.

Caro-Moniez, M., 1962. Sur un niveau à spores du Dévonien Supérieur du sondage de Tournai (Belgique). Ann. Soc. Géol. Nord, 82: 111—115.

Chaloner, W.G., 1951. On *Spencerisporites*, gen, nov., and *S. karczcewskii* (Zerndt), the isolated spores of *Spenceritis insignis* Scott. Ann. Mag. Nat. Hist., 12(4): 861—873.

Clayton, G., Coquel, R., Doubinger, J., Gueinn, K.J., Loboziak, S., Owens, B. and Streel, M., 1977. Carboniferous miospores of Western Europe: Illustration and zonation. Meded. Rijks Geol. Dienst, N.S., 29: 1—71.

Clayton, G. and Graham, J.R., 1974. Miospore assemblages from the Devonian Sherkin Formation of southwest County Cork, Rep. of Ireland. Pollen Spores, XIV(4): 565—588.

Clayton, G., Higgs, K., Gueinn, K.J. and Van Gelder, A., 1974. Palynological correlations in the Cork beds (Upper Devonian—?Upper Carboniferous) of southern Ireland. Proc. R. Ir. Acad., B 74(10): 145—155.

Clayton, G., Higgs, K., Keegan, J.B. and Sevastopula, G.D., 1978. Correlation of the palynological zonation of the Dinantian of the British Isles. Palinologia, (num. extraord.) 1: 137—148.

Evans, P.R., 1970. Revision of the miospore genera *Perotrilites* Erdtmann ex Couper 1953 and *Diaphanospora* Balme et Hassell 1962. Aust. Bur. Min. Resour. Geol. Geophys. Bull., 116: 65—74.

Gardiner, P.R.R. and Horne, R.R., 1972. The Devonian and Lower Carboniferous clastic correlatives of southern Ireland. Geol. Surv. Irel. Bull., 1: 335—366.

Gardiner, P.R.R. and Horne, R.R., 1976. The Devonian and Lower Carboniferous clastic correlatives of southern Ireland, some modifications. Geol. Surv. Irel. Bull., 2: 79—84.

Gayer, R.A., Allen, K.C., Bassett, M.G. and Edwards, D., 1973. The structure of the Taff Gorge area, Glamorgan, and the stratigraphy of the Old Red Sandstone—Carboniferous Limestone transition. Geol. J., 8(2): 345—374.

Higgs, K., 1975. Upper Devonian and Lower Carboniferous miospore assemblages from Hook Head, County Wexford, Ireland. Micropaleontology, 21: 393—419.

Hoffmeister, W.S., Staplin, F.L. and Malloy, R.E., 1955. Mississippian plant spores from the Hardinsburg Formation of Illinois and Kentucky. J. Paleontol., 29(3): 372—399.

Hughes, N.F. and Playford, G., 1961. Palynological reconnaissance of the Lower Carboniferous of Spitsbergen. Micropaleontology, 7(1).

Ishchenko, A.M., 1952. Atlas of microspores and pollen of the Middle Carboniferous of the western part of the Donetz basin. Izd. Akad. Nauk Ukrainian S.S.R., Inst. Geol. Nauk., pp.1—83 (in Russian).

Jansonius, J. and Hills, L.V., 1976. Genera file of Fossil Spores and Pollen. Special Publication, Dep. Geol., University of Calgary, Alta.

Keegan, J.B., 1977. Late Devonian and Early Carboniferous miospores from the Galley Head—Leap Harbour region of southwest Ireland. Pollen Spores, XIX(4): 545—573.

Kedo, G.I., 1957. Spores from the supra-salt Devonian deposits of the Pripyat Depression and their stratigraphic significance. Paleontol. Stratigr., B.S.S.R., Minsk, Akad. Nauk B.S.S.R., 1: 5—47 (in Russian).

Kedo, G.I., 1974. New spore forms from the Upper Devonian of the Pripyat Depression. In: V.K. Golubtsov and S.S. Manjkin, (Editors), Paleozoic Spores of Byelorussia (Pripyat Depression). NIGRI, Minsk. pp.3—74 (in Russian).

Kedo, G.I., Nazarenko, A.M., Nekrjata, N.S., Raskatova, L.G., Sennova, W.F. and Tchibrikova, E.W., 1971. New spore forms from Famennian beds of the Pripyat Depression, Central districts of the Russian Platform, Volga—Ural gas and oil province and Timan. In: V.K. Golubtsov (Editor), Palynological Research in Byelorussia and Other Regions of the U.S.S.R. Nauka i Technika, Minsk, pp.172—205 (in Russian).

Leisman, G.A., 1962. A *Spencerites* sporangium and associated spores from Kansas. Micropaleontology, 8(3): 396—403.

Mortimer, M.G. and Chaloner, W.G., 1972. The palynology of the concealed Devonian rocks of southern England. Bull. Geol. Surv. Gr. Br., 39: 1—56.

Naumova, S.N., 1953. Spore and pollen assemblages from the Upper Devonian of the Russian Platform and their stratigraphic significance. Tr. Inst. Geol. Nauk Akad. S.S.S.R., 143(Geol. Ser., 60): 1—204 (in Russian).

Naylor, D., Higgs, K. and Boland, M.A., 1977. Stratigraphy on the north flank of the Dunmanus Syncline, West Cork. Geol. Surv. Irel. Bull., 2(2): 143—158.

Naylor, D., Jones, P.C. and Clayton, G., 1978. The Namurian stratigraphy of Whiddy Island, Bantry Bay, West Cork. Geol. Surv. Irel. Bull., 2: 235—253.

Nazarenko, A.M., Kedo, G.I., Araslanova, R.M., Zjdanova, L.J., Lomaeva, E.T., Raskatova L.G., Sennova, V.F., Sergeeva, L.A., Umnova, V.T. and Chichova, G.M., 1971. New spore forms from Frasnian beds of the Russian Platform and Altai. In: V.K. Golubtsov (Editor), Palynological Research in Byelorussia and Other Regions of the U.S.S.R. Nauka i Technika, Minsk, pp.155—172 (in Russian).

Nekrjata, N.S., 1974. Spore complexes from Lower Famennian (intersaline) beds from the Pripyat Depression and their stratigraphic value. In: V.K. Golubtsov and S.S. Manjkin (Editors), Paleozoic Spores of Byelorussia (Pripyat Depression) NIGRI, Minsk, pp. 73—81 (in Russian).

Paproth, E. and Streel, M., 1970. Corrélations biostratigraphiques près de la limite Dévonien/Carbonifère entre les faciès littoraux ardennais et le faciès bathyaux rhénans. In: Coll. Stratigraphie Carbonifère. Congr. Coll. Univ. Liège, 55: 365—398.

Richardson, J.B., 1965. Middle Old Red Sandstone spore assemblages from the Orcadian basin, North-east Scotland. Paleontology, 7: 559—605.

Schopf, J.M., Wilson, L.R. and Bentall, R., 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. Rep. Inv. Ill. State Geol. Surv., pp.1—72.

Streel, M., 1964. Étude palynologique du Dévonien du sondage de Booischot (Belgique), note préliminaire. Bull. Soc. Belge. Géol., LXXIII: 172—190.

Streel, M., 1969. Corrélations palynologiques entre des sédiments de transition Dévonien/Dinantien dans les bassins Ardenno-Rhénans. C. R. VI. Int. Congr. Stratigr. Géol. Carbonifère, Sheffield, I: 3—18.

Streel, M., and Traverse, A., 1978. Spores from the Devonian/Mississippian transition near the Horseshoe Curve section, Altoona, Pennsylvania, USA. Rev. Palaeobot. Palynol., 26: 21—40.

Turnau, E., 1975. Microflora of the Famennian and Tournaisian deposits from boreholes of northern Poland. Act. Geol. Pol., 25: 505—528.

Urban, J.B., 1968. *Dibrochosporites*, a new sporomorph from the Middle Devonian of Iowa. Micropaleontology, 14(3): 371—375.

Van der Zwan, C.J., 1979. Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland: I. The *Cyrtospora cristifer* morphon. Rev. Palaeobot. Palynol., 28: 1—20.

Van der Zwan, C.J., 1980a. Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. II. The *Auroraspora macra* morphon. Rev. Palaeobot. Palynol., 30: 133—155.

Van der Zwan, C.J., 1980b. Aspects of Late Devonian and Early Carboniferous palynology of southern Ireland. III. Palynology of Devonian—Carboniferous transition sequences with special reference to the Bantry Bay area, Co. Cork. Rev. Palaeobot. Palynol., 30: 165—286.

Van der Zwan, C.J. and Van Veen, P.M., 1978. The Devonian—Carboniferous transition sequence in southern Ireland: Integration of palaeogeography and palynology. Palinologia, 1: 469—479.

Visscher, H., 1971. The Permian and Triassic of the Kingscourt outlier, Ireland — a palynological investigation related to regional stratigraphical problems in the Permian and Triassic of Western Europe. Geol. Surv. Irel., Spec. Pap., 1: 114 pp.

Winslow, M.R., 1962. Plant spores and other microfossils from Upper Devonian and Lower Carboniferous rocks of Ohio. Prof. Pap. U.S. Geol. Surv., No.364: 93 pp.